Plankton of the central Great Barrier Reef: abundance, production and trophodynamic roles

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The abundance, composition and metabolic activity of plankton were assessed in the Tribulation zone of the central Great Barrier Reef (16°–17°S). Wet phytoplankton biomass ranged in shallow reef waters from 30 to 70 mg m^{-3}, and from 60 to 270 mg m^{-3} in the deep lagoon and in the estuarine areas which are dominated by pico- and nano-algae. Wet bacterioplankton biomass varied from 70 to 290 mg m^{-3}. Wet meroplankton biomass was less than 10 mg m^{-3}. Wet daytime mesozooplankton biomass ranged from 100 to 300 mg m^{-3} in the deep lagoon. In the estuarine area, it reached 400 to 1300 mg m^{-3} and in the shallow inner lagoon of the Low Isles ring reef it varied from 10 to 30 mg m^{-3}. Zooplankton density increased at night and was 3 to 5 fold greater in the deep lagoon, for about 2 orders of magnitude greater over the reef shallows and up to 3 orders of magnitude greater in mangrove habitats, due to the emergence of demersal components from the benthos. The biomass of zooplankton hidden in the benthic substrates during the day reached 10 to 40 g m^{-2}. Pelagic primary production in the deep lagoon varied between 0.2 and 0.5 g C m^{-2} d^{-1}. A calculation of the energy balance suggests that the basic energy source for heterotrophic plankton production in the deep lagoon is the organic matter exported from surrounding reef benthic communities and from mangroves. The trophic status of coral reef pelagic ecosystem might range from mesotrophic to eutrophic.

Keywords: reef, microplankton, bacterioplankton, mesoplankton, trophodynamics, demersals

INTRODUCTION

Coral reef fauna is known to be dominated by planktivore animals (Harmelin-Vivien, 1981; Sorokin, 1990, 1993). Phytoplankton and heterotrophic microplankton provide nutrition for numerous pelagic and benthic filterers and sediment feeders. Zooplankton forms a basic food source for various pelagic predators like fish larvae, planktivorous and omnivorous fish, pelagic and benthic coelenterates, bryozoans, tunicates and for the corals themselves. Consequently, the trophodynamics of the coral reef ecosystems depends critically on plankton dynamics progress in the waters surrounding coral reef. The interaction between reef and surrounding waters is poorly understood and plankton studies on coral reefs need yet to address the principal problem of coral reef ecology, which suggests a discrepancy between low pelagic productivity of oligotrophic coral reef waters (Furnas, 1991) and the abundance and diversity of reef planktivore fauna. There are three principal causes of this imbalance: (a) an underestimation of the contribution of microheterotrophs to the production of particulate food; (b) an underestimation of mesozooplankton standing stock; and (c) that only plankton production (not just the standing stock) is available for reef planktivore fauna.

This imbalance has also been suggested in recent publications on primary production and plankton abundance in the waters of the central Great Barrier Reef (GBR) (Moriarty *et al.*, 1985; Jacoby & Greenwood, 1988; Furnas & Mitchell, 1990; Roman *et al.*, 1990; Brodie *et al.*, 1997; McKinnon *et al.*, 2005). To address this, we undertook an investigation of plankton abundance and productivity in this area of the GBR in the summer 1999–2000. We assessed the standing stocks and production of the principal groups of micro- and mesoplankton including the benthos–planktonic demersal component. Whole plankton respiration and concentrations of labile organic matter, suspended organic matter and total phosphorus were also measured in order to disclose the allochthonous energy and nutrient sources involved in the creation of plankton production in reef waters. The relative importance of autochthonous and allochthonous energy sources in reef pelagic communities was also assessed (Sorokin, 1990; Venier & Pauly, 1997). We also intended to compare the concentration of microplankton and zooplankton thus far recorded in reef waters with the known threshold limits for the nutrition of filtering, seston feeding and predatory reef planktivore fauna. This kind of comparison provides an additional way to verify the reliability of the data on plankton abundance.

MATERIALS AND METHODS

Field research was undertaken between November 1999 and February 2001 at the Low Isles Research Station of the

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University of Queensland. The sampling area covered the principal habitats in the Tribulation zone of the central GBR between 16° and 17°S. Basic cross-sections began in the estuarine area of the Mosman River (depth-range 6 to 12 m) and then crossed the deep lagoon up to the Batt Reef (Station 6). Station 5 was situated in the boat channel 28 m deep, 3 miles to the east of Low Isles reef (Figure 1A). The inner lagoon of Low Isles reef 1.5 to 1.8 m deep was sampled during high tide (Figure 1B). Mangrove habitats were sampled in the mangrove forest site of Low Isles reef (Figure 1B) and in the intertidal Daintree River, which crosses the coastal mangrove forest (Figure 1C). The basic cross-section was sampled 3 times. Each sampling mission was carried out in daytime and at night. Time series sampling was also undertaken in the inner lagoon and at its external margins to investigate diel migrations of zooplankton.

The selection of analytical methods used was based upon our former experience (Sorokin, 1999). The stock of labile organic matter (LOM) was estimated via the measuring of BOD-25. Total phosphorus was analysed in the intact water samples fixed with 0.5 ml 10 N H_2SO_4 after persulphate oxidation of seston (Parsons et al., 1984). The microplankton was quantified within its principal groups: bacterioplankton, phytoplankton, planktonic protozoa and metazoan larvae. Wet biomass of the microplankton components was assessed as equal to their biovolume calculated after the number of cells per 1 m^{-3} and mean cell volume expressed in μm^3. In this case, 10^9 μm^3 correspond to 1 mm^3 of biovolume or to 1 mg of wet biomass. Bacterioplankton, phytoplankton zooflagellates and nano-ciliates were quantified by epifluorescence microscopy afterwards (Hobbie et al., 1977; Caron, 1983). Ciliates >30 μm size were quantified by viable counting in a chamber 4 mm deep with 30 cm^3 capacity (Sorokin, 1999). Metazoan larvae were collected using a 40 μm net.

The mesozooplankton was collected in the shallows by filtering 50 l of water taken with a bucket through a net with a 40 μm mesh (Glynn, 1973; Sorokin, 1990, 1994). In the deep lagoon, a Juday's type 120 μm mesh net was towed vertically. The upper ring diameter for this net was 20 cm and 30 cm for the lower ring. The samples were fixed with Lugol solution
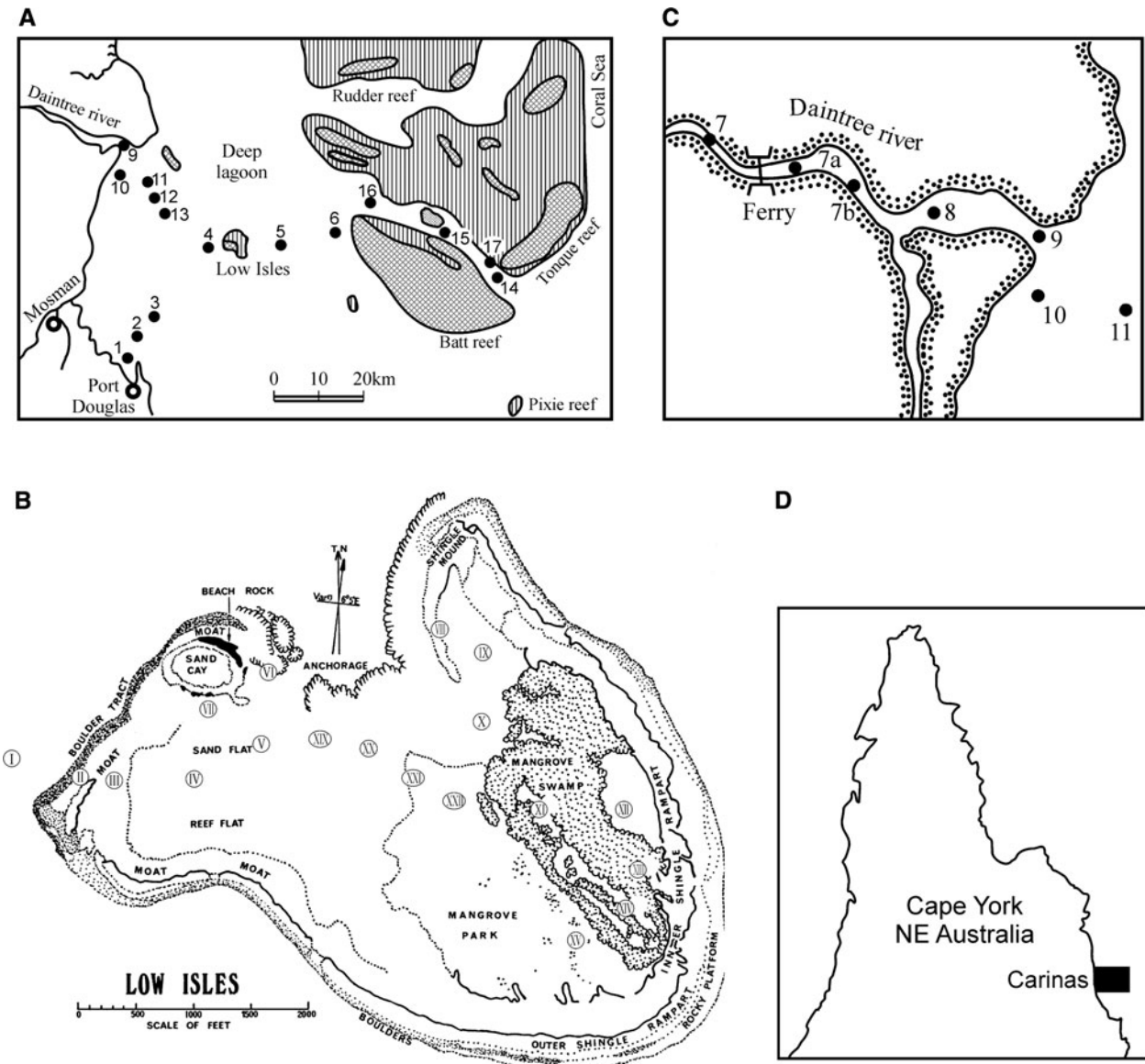

Fig. 1. Schemes showing the position of the stations: A, at the main cross-section; B, in the Low Isles lagoon and reef; C, in the intertidal Daintree River and estuary.

and were processed over several days using a 5 mm deep, 50 cm^3 round plastic chamber with the bottom lined with intervals equal to the diameter of a field stereoscope. The chamber was filled with the sample without air bubbles. The total wet biomass of mesozooplankton (mg m^{-3}) was assessed as the sum of biomasses of its key size-taxonomic groups, which were calculated accounting for the numerical abundance of each group expressed as ind. per 1 m^3 of water filtered and the mean individual weight of plankters.

The volume of water filtered by the net was calculated knowing the tow length and the area of the upper ring. The mean individual weights of some zooplankters are given in Table 1. The weight of demersal zooplankton was measured directly using a sensitive balance.

The catching efficiency of towing plankton nets is generally less than 100% (Sorokin & Pavelyeva, 1972; Sorokin, 1990). Therefore, each net has to be calibrated for its efficiency. We calibrated our Juday's net as follows. The net was fixed within the frame with floats attained to keep the net in a horizontal position at a depth of 30 cm under the water surface. The net was towed for 20 m in the inner and also the deep lagoons. Before and after towing, 100-l of water collected in the bucket was filtered through a 40 μm plankton net to obtain a reference sample. The catching efficiency was calculated as the percentage ratio of total biomass (mg m^{-3}) and total number (ind. m^{-3}) of zooplankton assessed in the net sample to those found in the reference sample. The calibration procedure was repeated five times. The mean catching efficiency of this net was thus assessed at 50% in relation to the zooplankton number, at 60% in relation to its total biomass, at 54% in relation to the copepod biomass and 70% in relation to the biomass of chaetognaths.

The biomass of the whole bentho-planktonic community which hide during the day time in the bottom substrates like macrophytes or coral rubble was assessed as follows. The samples of such substrates were gently collected and placed underwater in the plastic bags. The pre-weighed samples were subsequently thoroughly washed in 2 volumes of water to wash out the hidden fauna. Then both washes were filtered via a 200 μm mesh net to separate and to quantify the washed out plankters.

Phytoplankton primary production was measured with a version of the radiocarbon technique (Sorokin, 1999). Glass bottles (400 ml) were used for the *in situ* incubations which lasted 3 to 4 hours. The respiration rate was determined with the oxygen bottle method. Dark bottles (400 ml) were incubated at the *in situ* temperature. Dissolved oxygen was

measured with the Winkler method. Bacterial production (P$_b$) was calculated after the decomposition rate (D) expressed as mg C m^{-3} d^{-1}: P$_b$ = 0.28 D mg C m^{-3} d^{-1}. This coefficient (0.28) was adapted experimentally for the reef waters by measuring the ratio of bacterial production to decomposition rate D, both expressed in the carbon units, in the same water sample. The bacterial production was assessed in this case with the use of the dark CO$_2$ uptake method (Sorokin, 1999).

RESULTS

Microplankton composition and biomass

Phytoplankton biomass in waters of the deep lagoon ranged from 120 to 150 mg m^{-3} (Table 2). In the estuarine areas, it varied ranging from 130 to 345 mg m^{-3}. Pico-fraction was dominated by *Synechococcus* and *Prochlorococcus*. Nano-algae were mainly represented by chrysomonadic flagellates. Random trichomes and colonies of *Trichodesmium* were also present in the zooplankton samples collected with a 40 μm net. However, a large floating slick of *Trichodesmium* had drifted into the lagoon on 9 February as there was a strong easterly wind. The slick appeared 1 to 2 km to the north of the Low Isles reef and reached the continental coast the next day. The biomass of *Trichodesmium* in this slick was 0.75 g m^{-3}, the surface primary production 0.1 g C m^{-3} d^{-1} and the specific production nearly 0.1 per day, compared to 1 to 2 in the pico- and nanophytoplankton fraction. This suggests that the *Trichodesmium* in the drifting slick was senescent.

Bacterioplankton numbers ranged in the reef waters from 0.6 to 3.5 × 10^6 cells ml^{-1} (Table 3), and the wet biomass between 88 and 440 mg m^{-3} (Table 2). This density was close to the phytoplankton biomass or exceeds it by 2 to 3 times. In the estuarine waters, the biomass of bacteria reached over 300 mg m^{-3}. The protozoan community was dominated by zooflagellates and oligotrichia ciliates. The number of zooflagellates ranged from 0.5 to 16 × 10^6 cells l^{-1}, and their wet biomass was from 2 to 20 mg m^{-3}. The number of ciliates ranged from 2 to 18 × 10^3 cells l^{-1}, and their biomass from 6 to 100 mg m^{-3} (Tables 2 & 3). The biomass of meroplanktonic larvaceans (nauplii and trochophores) was most often less than 10 mg m^{-3}. The number of nauplii in the deep lagoon varied from 0.5 to 6.0 × 10^3 m^{-3} (Table 3).

Mesozooplankton was abundant in the Mosman estuarine zone at Stations 1 and 2, even during daytime. Its numbers ranged from 11 to 28 × 10^3 ind. m^{-3} and biomass from 650 to 1260 mg m^{-3}. At night, the biomass increased from 840 to 2320 mg m^{-3}. The water column biomass at these stations was nearly 7 g m^{-2} during the daytime, increasing up to 10 to 16 g m^{-2} at night (Table 2). The demersal fraction, being represented mostly by mysids and amphipods, contributed 30 to 60% of the nocturnal zooplankton biomass. In the deep lagoon at Stations 5 and 6, the daytime zooplankton biomass was between 200 and 400 mg m^{-3}, or 35 to 70 mg m^{-3} of the dry weight, assuming a dw/ww ratio 0.18 (Petipa, 1977). At night, the zooplankton biomass increased 2 to 3 times, attaining 700 to 890 mg m^{-3}, with a numerical density up to 16 ind.10^3 m^{-3} (Tables 2 & 3). The daytime water-column biomass was 5 to 15 g m^{-2} in this area. At night, it reached up to 32 g m^{-2}. The demersal fraction contributed 30 to 50% of

Table 1. Ranges of individual wet weights (W) of the principal zooplankton groups (based on Glynn, 1973; Afrikova *et al.*, 1977).

Zooplankton groups	Range of body length, mm	W, mg ind.$^{-1}$
Nauplii of copepods	0.06–0.12	0.04–0.4
Small copepods	0.3–0.5	8–15
Medium size copepods	0.6–1.0	20–40
Large copepods	1.1–2.5	50–200
Cladocerans	0.8–1.2	35–60
Appendicularians, larvae	0.8–2.0	10–25
Zoea	1.0–2.0	50–150
Mysids	2.0–4.0	120–400
Amphipods	3.0–6.0	400–1500
Chaetognaths larvae	3.0–4.0	100–200

Table 2. Whole plankton density and its composition estimated during the daytime and at night in the principal habitats of the central Great Barrier Reef November–January; abbreviations for dominant zooplankton groups: cp, copepods; ch, chaetognath larvae; ap, appendicularia larvae; os, ostracods; ms, mysids; zo, zoea; am, amphipods, pl, polychaetes; nm, nematods; jl, jelly plankton. All data are given as wet biomass.

Habitats	Time of the day	Microplankton (means)				Mesozooplankton				Whole plankton biomass, (WPB), mg m^{-3} (means)
		Phytoplankton, mg m^{-3}	Bacterio-plankton, mg m^{-3}	Planktonic protozoa, mg m^{-3}	Share in WPB, %	mg m^{-3} (means)	g m^{-2} (ranges)	Share of demersals, % (means)	Domination	
Deep lagoons; Stations 4, 5 & 6	Daytime	126	105	70	48	321	5.5–15.0	14	cp, ch, ap, am, jl	622
	night	155	160	105	34	802	16.2–32.1	54	ms, cp, ch, am, ap	1222
Channel between Batt and Tonque outer Barrier reefs, Stations 14, 15 & 16	Night	155	115	112	22	1280	24.2–87.1	23	ch, cp, ap, ms, os	1684
Estuarine area of Mosman River, Stations 1, 2 & 3.	Daytime	174	112	67	35	580	7.0–7.5	6	ch, cp, jl, ms	962
	night	62	175	108	18	1540	10.1–16.2	42	cp, am, ms, cp, jl	1885
Estuarine area of Daintree river, Stations 9 & 10 (salinity 14–20)	Daytime	345	360	86	57	607	2.9–5.6	45	cp, ch, ms, zo, ap	1400
	night	135	440	92	29	1650	10.3–11.2	52	ms, cp, zo, am, ch, ap	2317
Low Isles inner lagoon; Stations 2, 4 & 6 (high water)	Daytime	46	88	122	90	26	0.005–0.01	12	cp, ch, ap, zo	282
	night	55	114	102	15	1550	0.45–0.87	77	ms, zo, cp, ap	1820
The same (low water), Stations 20 & 21	Night	35	271	58	31	806	0.32–0.38	80	zo, ms, os, cp, pl	1170
Low Isles mangrove forest, Stations 12 & 14	Daytime	58	200	45	84	48	0.02–0.03	21	cp, pl, nm, ap	357
	night	34	750	290	30	2515	0.60–1.42	75	cp, pl, ap, nm	3594
Intertidal Daintree River, Stations 7, 7a & 8 (beginning of ebb)	Daytime	903	754	62	99	17	0.07–0.10	75	ms, cp	1736
	night	185	712	84	21	3760	14.2–37.7	5	cp, ms, am	4741

Table 3. Numerical density of basic plankton components in the research sites given as range sampled at the stations; d-r, depth-range.

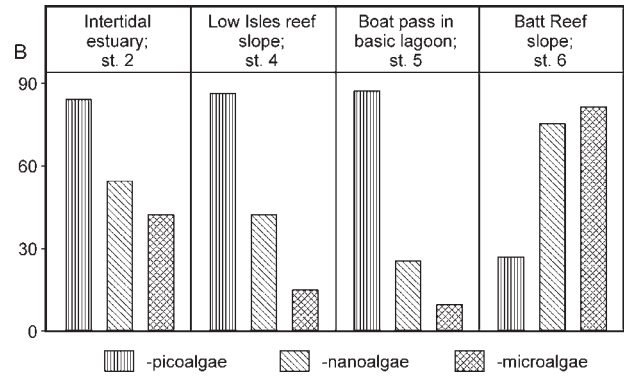| Plankton components	Main Great Barrier Reef lagoon		Low Isles inner lagoon and reefs				Daintree River and estuary
	Estuarine zone; d-r = 6–12 m	Open deep lagoon; d-r = 20–36 m	Lagoon itself, d-r = 0.5–2 m		Mangrove pools, d-r = 0.4–1.5 m		High water
			High water	Low water	High water	Low water	
Phytoplankton, (daytime)							
Picoalgae, 10^3 ml^{-1}							
Cyanobacteria	46–97	28–150	19–38	17–50	38–50	2–3	0–150
Eukaryotic	6–18	3–28	0.05–0.30	0.2–2.0	0.4–0.5	<0.2	0.3–38
Nano-algae, 10^3 ml^{-1}	0.6–3.0	0.2–1.8	0.3–0.6	0.3–2.0	0.5–0.6	0.6–0.8	0.1–2.5
Microalgae, 10^3 l^{-1}	3–18	1.5–7.5	3–5	4–8	3–4	4–7	0–220
Microheterotrophs, (daytime)							
Bacterioplankton, 10^6 ml^{-1}	1.2–2.3	0.8–2.1	0.8–1.1	0.4–0.9	0.7–0.9	1.8–3.5	1.5–4.8
Zooflagellates, 10^6 l^{-1}	1.4–2.0	2.8–16	1.4–2.0	0.6–1.5	0.5–1.5	0.6–6.3	0.6–6.0
Ciliates, 10^3 l^{-1}	7.5–18.6	4.8–12.3	8–18	2–9	4–6	6–14	2.5–45.5
Nauplii, ind. l^{-1}	2–8	0.5–6.0	0.2–2.0	0–0.1	0.2–0.5	<0.1	0.5–3.5
Mesozooplankton, 10^3 m^{-3}							
daytime	11–28	4–10	0.5–1.5	1.5–2.2	3–8	1.4–6.0	0.04–37.6
night	12–42	9–20	8–16	62–80	9–25	9–65	30–192

Fig. 2. Biomass (B, mg m^{-3}, wet weight) of phytoplankton size fractions at the main cross-section stations .

the nocturnal zooplankton biomass (Table 2; Figure 3). The greatest values of 1935 mg m^{-3} and 87 g m^{-2} in the water column were recorded at night at Station 14, taken at the outer barrier in the pass between Batt and Tongue reefs at a depth of 45 m.

The shallow inner lagoon of the Low Isles ring reef is 1.5 to 2 m deep at high tide, and 0.2 to 0.7 m during the ebb. The daytime zooplankton density over the seagrass–rubble bottom was between 1.5 and 2.2 × 10^3 ind. m^{-3} and its wet biomass between 9 and 30 mg m^{-3}. At night, it increased 10 to 100 fold, attaining 1 to 4 g m^{-3} (Tables 2, 3 & 4). However, the maximal daytime zooplankton density was recorded during the afternoon ebb over the margins of sand–grass flat 5 to 10 cm deep at a water temperature 37 to 39°C and oxygen saturation of over 200%. The zooplankton density attained there was 45 × 10^3 ind. m^{-3} and the biomass was 710 mg m^{-3}.

The data on the dynamics of demersal zooplankton during the night (Table 4; Figures 3 & 4) suggest that only a part of this community appear in the water column during the night. It means that its real density should be at least 3–5 times greater than that accounted for in the nocturnal samples in the inner lagoon or in the adjacent reef shallows outside. This concentration is supported by the results for the quantification of bentho-planktonic demersals hidden during the daytime in the typical bottom substrates of reef shallows (Table 5). Their biomass appeared to be about one order of magnitude greater than could be accounted for during nocturnal sampling. The wet biomass of this zooplankton fraction reached 20 to 40 g m^{-2}. Copepod populations increased rapidly as darkness fell. The most common were *Pseudocalanus, Tigriopus, Tisbe* and miscellaneous harpacticoid copepods. Demersal behaviour features are also displayed by some common neritic calanoid copepods (Hamner & Carleton, 1979).

Stock and dynamics of organic matter

The same parameters were measured at key stations in the deep lagoon and in the Low Isles lagoon (Table 6). Surface phytoplankton primary production was greatest in the Mosman estuarine area at Stations 1 to 3, ranging between 41 and 133 mg C m^{-3} d^{-1} (mean 72 mg C m^{-3} d^{-1}). In the deep lagoon, primary production was 20 to 32 mg C m^{-3} d^{-1}. This is a typical level for GBR lagoon waters, where the wet phytoplankton biomass is 80 to 250 mg m^{-3} and the chlorophyll
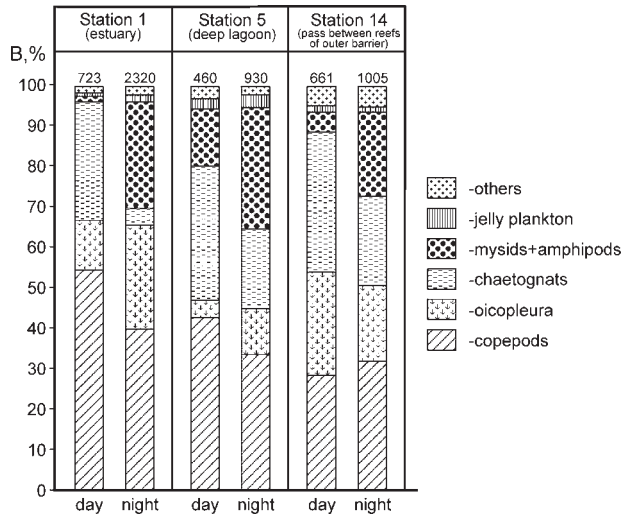
Fig. 3. Shares of zooplankton components in its total biomass at the main cross-section; numbers above the columns, wet zooplankton biomass, mg m^{-3}.

content 0.2 to 0.6 mg m^{-3} (Furnas & Mitchell, 1990; Liston *et al.*, 1992; Brodie *et al.*, 1997). The integrated primary production in the water column ranged between 0.18 and 0.48 g C m^{-3} d^{-1} (mean 0.36 g C m^{-3} d^{-1}), which corresponds to upper level in oligotrophic marine basins.

The decomposition rate corresponds to the whole plankton respiration rate and reflects the daily flux of labile organic matter. These parameters ranged between 0.32 and 0.62 mg O$_2$ l^{-1} d^{-1} or 84 to 165 µg C l^{-1} d^{-1} in the deep lagoon, and thus exceeding primary production by 1.3 to 5.0 times (Dc/Ps-ratio). The integrated decomposition rate in the water column ranged from 1 to 2.5 g C m^{-2} d^{-1}, which is 2.8 to 11.8 times greater than pelagic primary production (Dt/Pt ratio).

The standing stock of labile organic matter in the water (LOM) was nearly 1 mg C l^{-1} in the deep lagoon and approximately 2 mg l^{-1} in the estuarine zone. In the water column at Stations 3 to 6, it attained 1.9 to 3.6 g C m^{-2}. The share of LOM in total C$_{org}$ in marine waters is nearly 20 to 25% (Zsolnay, 1975; Torreton *et al.*, 2002). Thus, the total C$_{org}$ in reef water during high tide can be expected at 4 to 6 mg C l^{-1}. During the ebbs, it should be 10 to 14 C l^{-1}. LOM constitutes the principal energy source for pelagic and benthic heterotrophic production in the deep lagoon. The residence time of LOM (T) in the lagoon water was 8 to 15 days, thus suggesting an intensive turnover (Table 6).

Primary production in the inner lagoon during the high tide was similar to that in the deep lagoon, e.g. 20 to 35 mg C m^{-3} d^{-1}. During the ebb tide period, it decreased to 6 to 10 mg C m^{-3} d^{-1} (Table 6), while heterotrophic
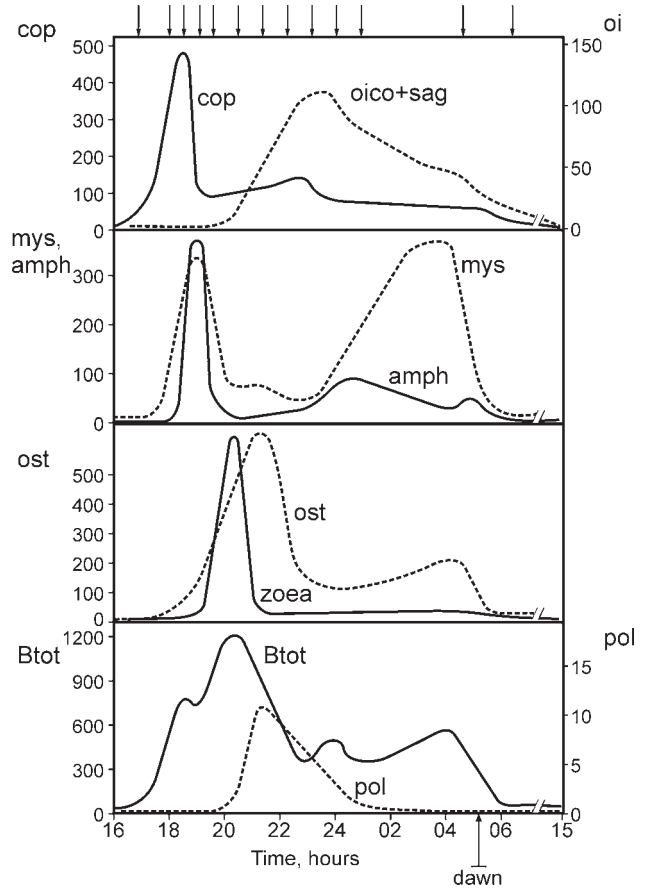

Fig. 4. Daily fluctuations of total zooplankton biomass (B$_{tot}$, mg m^{-3}) and of its principal groups at the slope of the Low Isles reef (Station 7a, 6m depth); abbreviations for the zooplankton groups: cop, copepods; chaet + app, chaetognath + appendicularian larvae; mys, mysids; amph, amphipods; ost, ostracods; pol, polychaetes: the arrows indicate the sampling times.

activity doubled. The decomposition rate ranged between 68 and 242 µg C l d^{-1} rising during the ebbs. These data suggest an exuding of excess benthic photosynthetic production, which is created by abundant macro- and microphytobenthos (Sorokin, 1993; Torreton *et al.*, 2002).

Plankton dynamics in the Daintree River and estuary

The intertidal Daintree River flows through a vast mangrove forest as it nears the coast. Tidal saline waters reach 4 to 6 km upstream. Three cruises undertaken in this area (at midday, late evening and midnight) coincided with the

Table 4. Change of zooplankton density and composition after sunset recorded during time series sampling at Station 6 (Pontoon) 6 m deep at the Low Isles windward coral reef 17.11.

Time	Holoplankton biomass, mg m^{-3}			Demersals biomass, mg m^{-3}			Total zooplankton	
	Copepods	Appendicularians+ chaetognath larvae	Cladocerans+ doliolids	Zoea	Mysids + amphipods	Ostracods	Number, 10^{3}m^{-3}	Biomass, mg m^{-3}
17.30	24	6	24	14	0	13	1.66	87
18.00	36	16	59	16	10	26	3.09	163
18.30	70	10	67	25	35	320	6.00	527
19.00	138	18	25	55	296	720	7.42	1252
19.30	174	15	19	990	120	2920	14.48	4238

Table 5. Numerical abundance (N) and biomass (B, g) of benthoplanktonic fauna contained in the bottom substrates of the Low Isles reef flats and in lagoon shallows; ww and dw, wet and dry weight units.

Site, depth at low water, (water temperature °C)	Kind of bottom sample, its weight (W)	Numerical abundance of key groups of fauna discovered in the samples (N)						Total number of bentho-planktonic fauna, 10^3, ind. m^{-2}	Its total wet biomass	
		Copepods, $N \cdot 10^3$ ind	Polychaetes, $N \cdot 10^3$ ind	Amphipods, $N \cdot 10^3$ ind	Decapods, N ind	Larvaceans (zoea and auricularians), N ind	Ostracods N, ind		g kg^{-1}	g m^{-2} of bottom area
Close to south-east shore; 15 cm (t° 36°C)	Sand with grass; W = 500 g	9.2	0.24	16	0	0	30	590	0.68	21.2
North-east coast of sandy island; 0.5 m	Coral rubble with ramose coralline algae and periphyton, W = 260 g	18.4	0.42	108	8	144	96	767	4.0	41.5
Same place, 0.6 m	Coral rubble with periphyton, W = 210 g;	2.3	0.35	0.46	5	32	10	211	1.0	12.6
Same; 0.8 m	Turbinaria + sargassum macrophytes on coral rubble; W = 510 g	10.1	1.7	0.52	7	0	18	770	1.1	36.1

Table 6. Mean values of standing stock of labile organic matter (LOM), its residence time (T), its production and decomposition rates in pelagic communities for principal habitats in the Tribulation zone of Great Barrier Reef.

Habitat		No. of stations con-sidered	Depth-range, m	LOM stock		Primary production		Decomposition rate		Bacterial production			Ratios	
				mg C l^{-1} (Lc)	T, days (Lc/Dc)	mg C m^{-3} d^{-1} (Ps)	g C $m^{-2}d^{-1}$ (Pt)	μg C l^{-1} d^{-1} (Dc)	g C m^{-2} d^{-1} (Dt)	μg C l^{-1} d^{-1}	g C m^{-2} d^{-1}	Dt/Pt	Specific production per day (μ)	
													By phyto-plankton	By bacterio-plankton
Deep lagoon		4, 5 & 6	21 – 36	0.98	10	27	0.36	94	2.46	27	0.73	6.8	1.3	1.4
Daintree and Mosman estuarine areas		1, 2, 3, 10 & 11	6 – 16	1.71	15	72	0.28	152	1.49	42	0.42	5.3	2.1	1.4
Low Isles inner lagoon	Low water	14 & 16	0.1 – 0.5	2.80	12	14	0.008	173	0.06	62	0.021	7.6	2.5	1.7
	High water	2, 4, 6, 9 & 12	1.6 – 1.9	1.50	14	25	0.04	124	0.20	33	0.063	5.2	3.1	0.6
Low Isles mangrove forest	Low water	13 & 14a	0.2 – 0.4	3.60	18	14	0.004	174	0.04	57	0.016	10.7	2.5	1.7
	High water	12 & 14	1.6 – 1.9	1.59	9	12	0.02	182	0.33	36	0.07	10.5	3.0	0.3
Daintree River		7, 8 & 9	4 – 6	1.94	9	313	0.90	227	1.14	6 2	0.32	1.4	3.1	0.6

beginning of the ebb. Fresh and brackish parts of the river contained an abundance of phytoplankton with a biomass of 390 to 940 mg m^{-3} and with photosynthetic production from 260 to 340 mg C m^{-3} d^{-1} (Tables 2 & 6). Most of the phytoplankton was small dinoflagellates, while in the mouth and estuarine areas, diatoms and symbiotic ciliates *Mesodinium rubrum* also appeared. Bacterioplankton in the river waters numbered over 2 × 10^6 cells ml^{-1}; its biomass was 300 to 800 mg m^{-3} (Tables 2 & 3). This was evidence that the river had been enriched with organic matter from the mangroves. Zooplankton was scarce in the river during the daytime (Station 7; Tables 2 & 3), but in the river mouth area and in the shallow turbid estuary filled with saline water (Stations 9 and 10), its daytime biomass increased from 700 to 800 mg m^{-3}. During darkness, the zooplankton biomass rose 200 to 300 fold in the river, and 3 to 5 fold in its mouth and estuarine areas. The copepods *Parvocalanus crassostris*, *Pseudodiaptomus griggae*, and small harpacticoids dominated in the river. At Station 7 their number reached 70 × 10^3 m^{-3} and at Station 8 170 × 10^3 m^{-3}, while in the daytime during the same tidal phase their numbers were only 110–130 ind. m^{-3} (Table 3). The mass of copepods of over 30 g m^{-2} might be hidden in the silted bed of the river. A greater part of their large nocturnal population, most probably, emerges from the bottom habitats of mangrove forest. Whole plankton biomass in the river at night reached 40 g m^{-2}. Discharges of this mass of plankton into the lagoon during the nocturnal ebbs create an important food stock for the planktivorous fauna and especially for the fish larvae, which tend to accumulate in the estuarine zones of intertidal rivers (Williams & Hatcher, 1983; Robertson *et al.*, 1988).

The pelagic community in the river and estuary was characterized by intense metabolic activity. The decomposition rate was 150 to 300 μg C l^{-1} d^{-1}, which was 3 to 4 fold greater than in the lagoon itself. The stock of labile organic matter found there was 1 to 2.3 mg C l^{-1} and its residence time 6 to 16 days (Table 6). Bacterial production in the river attained 60 μg C l^{-1} d^{-1}, or up to 400 mg m^{-3} d^{-1} of wet biomass.

Total phosphorus content in water

The content of total phosphorus (P$_{tot}$) in water is among the principal parameters characterizing the trophic status of an ecosystem and its availability of nutrient resources (unlike the content of dissolved inorganic phosphorus, which reflects only a temporal balance between its consumption and regeneration rates). The latter stays in the reef waters monotonously at a level close to limiting phytoplankton growth, e.g. 0.02 to 0.2 μM (Crossland, 1983). Mean P$_{tot}$ content measured at 40 stations was around 0.5 μM (Table 7). The contribution of P$_{tot}$ contained in the whole wet plankton biomass might be evaluated at a level of 0.15 to 0.25 μM, which corresponds to P$_{tot}$ content in the particulate matter in waters of the GBR lagoon (Liston *et al.*, 1992; Furnas *et al.*, 1997). In the Mosman River estuarine area in contact with the mangrove forest, the mean P$_{tot}$ content attained 0.75 μM. The same was observed in the Daintree River estuary and in the mangrove forest of the Low Isles reef. The phosphorus enrichment comes from the mangroves, where the population of nearly 50,000 New Guinea pigeons nest. The phosphorus enrichment of the water over the shallow bottom of its inner lagoon is also combined with the capability of the resident filtering fauna to accumulate P$_{tot}$ stock (Atkinson & Rigler, 1992; Sorokin, 1992, 1993).

Energy balance

The above data were used to create an energy balance approach based on the results of the biomass and production estimations expressed in energy units (kJ m^{-3}). This analysis was aimed at assessing food demand, production and metabolic activity of the principal food web components in basic kinds of reef ecosystems. Such a balance could also indicate energy sources for the reef fauna. Necessary data on the biomass and production of phytoplankton and bacterioplankton were obtained experimentally in the same way as the data on biomass of micro- and mesozooplankton (Tables 2 & 6). The latter was assessed as the sum of copepod biomass plus triple biomass of bentho-planktonic demersals measured in the nocturnal samples, meaning that only about a third part of their total population appeared at a given moment at night in the water column (see above). For the biomass of benthic components and fish, corresponding published data were used (McWilliam *et al.*, 1981; Sorokin, 1990, 1993). The production and food demands for reef fauna components were calculated with the use of recognized specific production coefficients (Table 8). The respiration

Table 7. Contents of total phosphorus in waters of Low Isles region.

Site, depth-range (dr.) station numbers (st.)	Place	Number of stations sampled	Ptot, μM	
			Limits	Means (+)
Main section off Port Dongfas across deep lagoon: dr. 6 to 36 m; st. 1 to 6.	Estuarine area	4	0.4–1.2	0.75
	Deep lagoon	9	0.3–0.9	0.45
Low Isles reef; dr. 0.4–06 m; st. 4 to 8; 13; 15; 23	Inner lagoon (high water)	3	0.2–0.4	0.32
	Same (low water)	6	0.5–0.9	0.60
	Mangrove forest (high water)	2	0.3–0.4	0.35
	Same (low water)	3	0.7–0.9	0.76
Daintree River; dr. 5–20 m; st. 8 to 12	Lower part of river	1	–	0.51
	River mouth	1	–	0.35
	Estuarine area	3	0.5–0.6	0.57
Cairns area (mean values, after Furnas *et al.*, 1997)	Inshore zone (< 20 m deep)	–	–	0.31 (0.12)
	Offshore zone (> 20 m deep)	–	–	0.24 (0.07)

(+) numbers in parentheses, size of particulate organic phosphorus fraction.

Table 8. Carbon and energy equivalents of wet biomass and convenient coefficients used for the calculation of energy balance in the reef ecosystem investigated; designations for the coefficients: K_2, efficiency of secondary production; I assimilability efficiency of ingested food, %; μ, specific production per day (P/B). Based on Sorokin (1993), Zaika (1973) Petipa (1977); Grese (1978).

Food web components	Percentage of C_{org} in wet biomass	Energy equivalents pf wet biomass, kj g	Coefficients		
			K_2	I	μ
Phytoplankton	11	4.3	–	–	–
Macrophytobenthos	9	3.5	–	–	–
Microphytobenthos	28	34	0.32	–	–
Bacterioplankton	18	7.7	0.32	–	–
Microzooplankton	9	3.5	0.50	0.7	1.0
Mesozooplankton					
Holoplanktonic copepods	9	3.5	0.35	0.7	0.2
Bentho-planktonic demersals	10	4.2	0.35	0.8	0.05
Benthic bacteria	15	6.0	0.25	–	0.2
Zoobenthos	11	4.3	0.20	0.6	0.015
Fish	12	48	0.30	0.8	0.002

rates (M) and ingested food ration (R) in heterotrophic food web components were calculated using known efficiency coefficients of secondary production (K_2), and of assimilability for consumed food (I), given Table 8. Thus, $M = P(I - K_2)/K_2$, and $R = M + P/I$.

Balances were calculated for the ecosystems of the deep and inner lagoons (Table 9). Corresponding models of energy fluxes in both these ecosystems were deduced by accounting for information on the nutrition of principal components of reef fauna (Pavlova *et al.*, 1971; Petipa, 1981; Grese, 1978; Sorokin, 1999). The principal food web components are interconnected in these models not only with each other but also with the pool of dead organic matter both dissolved and particulate (Figures 5 & 6).

An analysis of food balance and energy flux models in two of the most common reef biotopes demonstrates the key role of heterotrophic microplankton in the reef food webs, which

functions as the link between benthic primary producers (algae, seagrasses, corals and mangroves) and filtering fauna both in shallow and deep reef habitats (Sorokin, 1990, 1994; Venier & Pauly, 1997). The role of phytoplankton in food webs in the reef shallows appears to be secondary to that of the bacterioplankton and microzooplankton (Figure 6). However, in the deep lagoon it is quite significant, supplying up to 40% of the mesozooplankton food demand (Figure 5).

DISCUSSION

The phytoplankton population in central and northern GBR waters is usually dominated by pico-fraction (Crosbie & Furnas, 2001; Figure 2). The biomass of phytoplankton was low to moderate even in the deep lagoon: 60 to 270 mg m^{-3} (Table 2). This range is close to that calculated after the

Table 9. Biomass of food web components and energy balance in deep lagoon and shallow inner Low Isles lagoon ecosystems; designations for elements of food balance: R, food ration ingestion; A, assimilated part of food ration; P, production; M, metabolic losses; F, excretion.

Habitats	Food web components	Biomass		Elements of food balance equation, Kj m^{-2} d^{-1}					M/Mt ratio, %
		Wet weight, g m^{-2}	Kj m^{-2}	R	A	P	M	F	
Great Barrier Reef deep lagoon (20–30 m depth with sandy bottom)	Phytoplankton	3.5	15.1.	–	15.0	12.6	2.6	–	1.
	Microplankton	90	720.0	–	38.6	33.5	5.1	–	3
	Bacterioplankton	4.3	30.7	–	128.1	41.0	87.1	–	49
	Microzooplqnkton	21.0	7.4	24.7	17.3	8.0	9.3	6.1	5
	Mesozooplankton	42.0	47.7	40.5	34.2	12.6	22.2	7.9	13
	Benthic bacteria	10.0	60.0	–	36.0	9.0	27.0	–	15
	Zoobenthos	66.0	250.0	30.8	18.5	3.7	14.8	12.5	8
	Fish	40.0	192.0	15.6	12.6	3.8	8.8	2.6	5
Reef shallows, 2 to 5 m deep with bottom occupied by corals, coral rubble and macrophyte	Macro-, microphytoplankton and periphyton	500.0	1700.0	–	115.0	100.0	15.0	–	14
	Phytoplankton	0.07	0.3	–	0.8	0.7	6.1	–	6
	Bacterioplankton	0.20	1.5	–	5.9	1.9	4.0.	–	4
	Mesozooplankton	13.5	55.0	10.4	8.0	2.8	5.2	2.4	5
	Microzooplankton	0.13	0.5	1.4	1.9	0.5	0.5	0.4	0.4
	Benthic bacteria	15.6	90.0	–	63.0	18.0	54.0	–	52
	Zoobenthos	110.0	400.0	34.1	20.5	4.1	16.4	13.6	16
	Fish	40.0	186.0	15.3	12.3	3.7	8.6	3.0	2.6

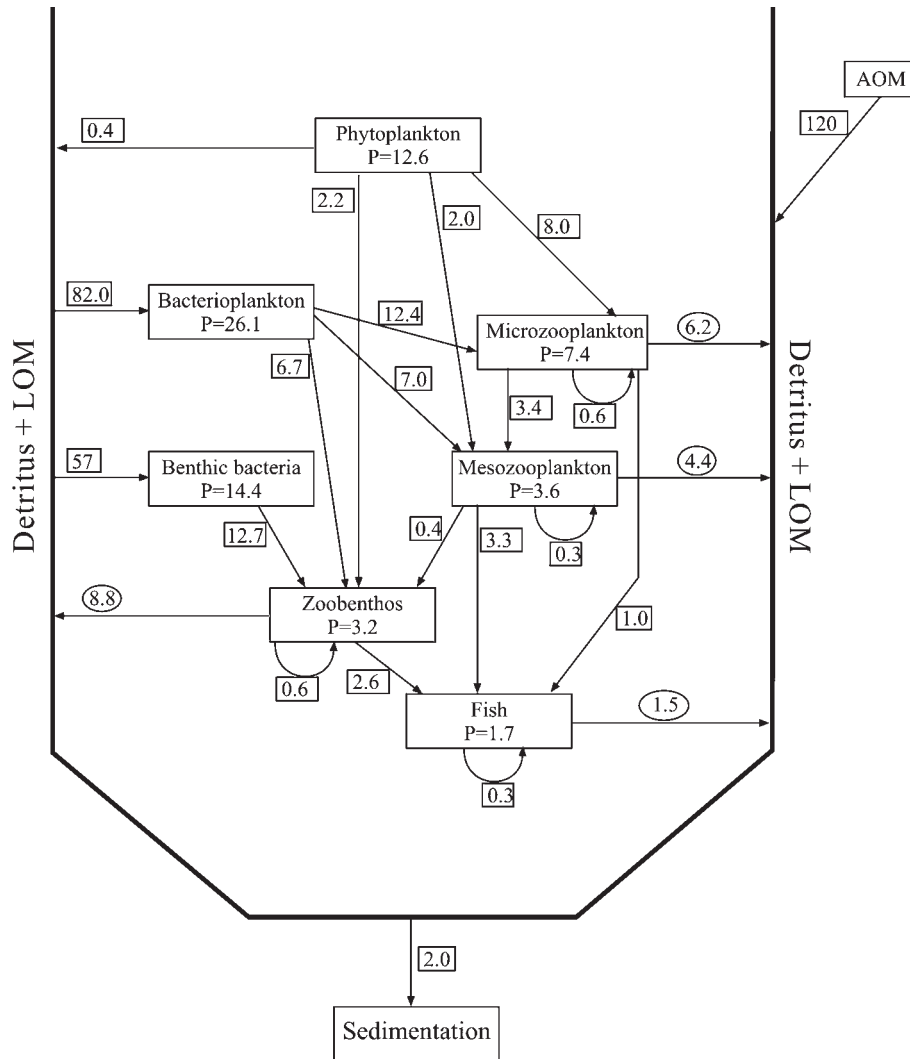**Fig. 5.** Energy flow scheme (kJ m^{-2} d^{-1}) in the deep Great Barrier Reef lagoon ecosystem; abbreviations: P, production; numbers in squares, food rations of subsequent food web components; numbers in ovals, non-digested food; numbers in trapezes, non-consumed food; AOM, allochthonous organic matter which arrives from the surrounding reefs, from the land, and from the Coral sea as drifting slicks of *Trichodesmium*; LOM, stock of dissolved labile organic matter in the water column.

chlorophyll data by Furnas & Mitchell (1990), e.g. the chlorophyll content between 0.2 and 0.6 mg m^{-3} corresponds to an approximate phytoplankton wet biomass of 60 to 240 mg m^{-3}. This level of phytoplankton density is typical of oligotrophic oceanic waters. The main cause of phytoplankton paucity is due to inorganic phosphorus deficiency in reef waters, where it is used by bacterioplankton and benthic vegetation (Sorokin, 1982; Crossland, 1983). However, primary production there was considerably high (0.1 to 0.4 g C m^{-2} d^{-1}), because of the high specific production of reef phytoplankton, dominated by pico- and nanoalgae (Crosbie & Furnas, 2001; Figure 2).

The biomass of *Trichodesmium*, might be considered a source of allochthonus organic matter and nutrients in the GBR ecosystem. Floating slicks of *Trichodesmium* appear periodically in the GBR lagoon, driven there from the Coral Sea. Such slicks are often formed along the eastern shores of ultra-oligotrophic tropical basins such as the Coral Sea, and the South China Sea. Young *Trichodesmium* populations grow as single trichomes in oligotrophic tropical seas at the upper boundary of thermocline. The aging cells form

coenobial bundles, which then float and lose their chlorophyll, gradually turning heterotrophic (Karnaukhov & Yashin, 2003). While accumulating in the surface film, they drift under the pressure of easterly trade winds and form dense slicks ('blooms') along the eastern shores which they encounter (Relevante *et al.*, 1982).

The joint wet biomass of microplankton in reef waters ranges between 300 and 600 mg m^{-3} (Table 2). Using a specific production over 1.5 per day (Tables 6 & 8), microplankton production might be expected to bee 0.5–1.0 g m^{-3} day. This level should be sufficient to meet the food demand of reef filterers and seston feeding fauna. The trophic status of the central GBR shelf waters is often misleadingly described as oligotrophic (Furnas, 1991), largely because of the low reported chlorophyll content in the water (<0.5 mg m^{-3}). However, most other indices suggest that it is rather eutrophic (Sorokin, 1990, 1994). Among such indices, the P$_{tot}$ content in water of 0.5 μM, the content of labile organic matter in water of 1.2 to 35 mg C l^{-1}, the decomposition rate in water of 70 to 240 μg C l^{-1} d^{-1}, the bacterioplankton production of 30 to 60 μg C m^{-3} d^{-1},
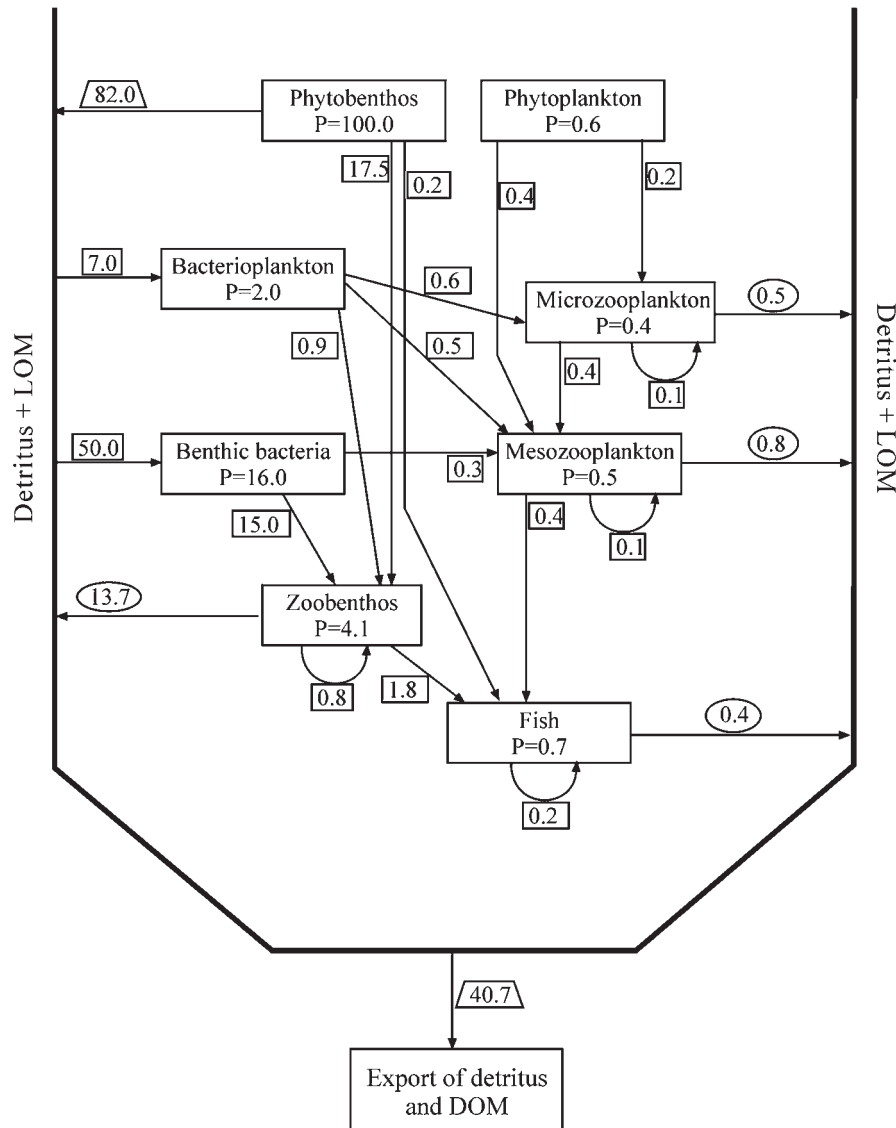
Fig. 6. Energy flow scheme (kJ m^{-2} d^{-1}) in the sand−grass flats ecosystem in the inner lagoon of Low Isles Reef; for designations see Figure 5.

the whole wet plankton biomass of 0.5 to 2.5 g m^{-3}, the nocturnal zooplankton biomass 1 to 4 g m^{-3} and the biomass of fish at 160 g m^{-2} should be considered when assessing the trophic status.

The coral reef ecosystems are intrinsically eutrophic judging by the level of their organic productivity, their abundant heterotrophic life and the intense nutrient fluxes (Kinsey, 1983, Sorokin, 1993). They are open systems interacting with the energy metabolism of whole shelf ecosystems. The involvement of external organic matter as the basic energy source for bacterial and protozoan production in the deep lagoon is evidenced by the ratio of decomposition to local primary production rates in its water column (Dt/Pp in Table 6). The decomposition rate greatly exceeds the pelagic primary production. The largest energy flux is driven by heterotrophic microplankton in the deep lagoon (Table 9; Figure 5). The latter creates a principal food source for zooplankton and benthic-filtering fauna (Pavlova et al., 1971; Sorokin, 1993). Production in the water column of the deep lagoon was significantly greater by microheterotrophs than by phytoplankton (Tables 6 & 9): being 0.67 to 0.85 g C m^{-2}, while primary production was 0.29 to

0.49 g C m^{-2} d^{-1}. The flux of organic matter supporting this production must therefore be largely of an allochthonous origin, while local pelagic primary production by phytoplankton could supply around 15% of energy needed (Figure 5); the rest might be supplied by external sources.

The principal flux of organic matter enters the lagoon from the surrounding vast shallow reefs. The export of exuded organic matter, organic aggregates, detritus and microbenthos living biomass from coral reefs is well documented (Marshall, 1968; Hansen et al., 1992; Sorokin, 1993; Ferrier-Pages et al., 1999; Torreton et al., 2002). The magnitude of this export may relate to the net autotrophic production of reef benthic associations. The limits of net production rates on barrier reefs may be evaluated between 3 and 8 g C m^{-2} d^{-1} against the background of gross primary production as between 5 and 11 g C m^{-2} d^{-1} (Barnes & Devereux, 1984; Sorokin, 1993; Pichon, 1997). Kinsey (1983) estimates the net photosynthetic production on the Rib reef of the central GBR close to 4.2 g C m^{-2} d^{-1}. Vast shallow reefs of the outer barrier are occupied by patch reefs and by sand-grass rubble and macrophyte flats with abundant periphytonic overgrowth. They cover

about 30% of the total shelf area in the Tribulation zone: 2500 km² out of 8000 km². With the most probable mean net benthic primary production in this area at 4 to 5 g C m^{-2} d^{-1}, the input of excess organic matter from this area into the waters of the deep lagoon might be expected at about 1.4 to 1.8 g C m² d^{-1}. Hansen *et al.* (1987) and Furnas & Mitchell (2001) estimate the contribution of the surrounding reefs to the primary production in the lagoon of the central GBR close to 50%, by the 10% coverage of shelf area by reefs. In the Tribulation zone it may be significantly greater. As an additional source of allochthonous organic matter the export of LOM and detritus from mangroves, the riverine discharge of detritus and plankton (Furnas & Mitchell, 2001) and the drifting *Trichodesmium* slicks can be considered.

Evaluation of zooplankton abundance in the GBR waters is difficult to carry out, although there are significant efforts to quantify it (McWilliam *et al.*, 1981; Hodgeson, 1982; Sammarco & Crenshaw, 1984; Hamner *et al.*, 1988; Roman *et al.*, 1990). The above publications use daytime vertical tows done with nets >200 μm mesh to evaluate mesoplankton biomass in the GBR waters and show limits of 1 to 10 mg C m^{-3} or around 10 to 100 mg m^{-3} wet weight. This seems to be between 5 times up to 1–2 orders of magnitude less than real (see Tables 2 & 4).

There is an underestimation in biomass determined in the above mentioned publications because no catching efficiency correction was used. The standard conical plankton nets undercatch the mesozooplankton between 2 to 10 times depending on the zooplankton composition and on the kind of a net (Sorokin & Paveljeva, 1972; Glynn, 1973; Sorokin, 1994). Specialists from the Shirshov Institute of Oceanology, RAS, have rejected use of these towing nets for zooplankton sampling in the ocean for the last 20 years. They used 140 l water samples taken with a large water bottle on the vertical profile and then filtered via 60 μm mesh net (Shushkina & Vinogradov, 2002), for this purpose, in the same way that was used to collect zooplankton in the reef shallows (Sorokin, 1990, 1994). Most of the standard plankton nets have meshes over 200 μm, and thus significantly under-catch small animals 0.15–0.25 mm wide. The latter became evident during our net calibrations (see Materials and Methods). The mesozooplankton fraction was represented mostly by small copepods and copepodides, and by slim appendicularian larvae. This fraction was almost absent in the parallel samples collected with the standard net 250 μm mesh. However, this fraction contributed to over 50% of zooplankton numerical density in the control samples. We have also calibrated the big conical net 275 μm mesh, which had been in use at the Low Isles Research Station since 1928. The catching efficiency of this net appeared to be 4% for the numerical density, and 20% for the biomass of the mesozooplankton.

Another probable cause of mesoplankton underestimating is the predominance of daytime tows during routine zooplankton sampling, notwithstanding the well-known abundance of demersals zooplankton in reef waters. The difference between the daytime and the nocturnal zooplankton biomass in the reef waters often attains 1 to 2 orders of magnitude (Glynn, 1973; Sale *et al.*, 1976).

McKinnon *et al.* (2005) used a double net supplied with a current meter. Their data appeared to be some 3 times greater than the above mentioned: 100 to 250 mg m^{-3} of wet biomass (10–25 mg C m^{-3}). However, it was also some 3 to 5 times an underestimation in comparison with our data (see

Table 2). The cause might be the 'bucket' effect induced by towing dense plankton nets with fine porosity (70 μm). In this case, the speed of the current and even its direction will be different in the centre of the net, where the current meter is fixed, and at its margins. Thus, the volume of water really filtered by the net might be much less then recorded by the current meter. For the correct measurement of water volume really filtered by the net, the current meter should be installed at its exit end as shown in Figure 7. Furthermore, the 'bucket' effect induces a pressure wave in front of the moving device, which should repel fast moving demersals like mysids or amphipods. This explains the small difference between the daytime and the nocturnal tows reported by the above authors. However, our results show that this difference is about 3 times in the deep lagoon and up 1 to 3 orders of magnitude over the reef shallows (Tables 2 & 4; Figure 4; Alldredge & King, 1977; Porter & Porter, 1977).

The information on mesoplankton abundance in the GBR waters presented in the literature is often insufficient (Hodgeson, 1982; Robertson *et al.*, 1988; Le Borgne *et al.*, 1989). For example, only numerical density is given, despite that the individual weights of plankters in this group varies within 2 orders of magnitude. The reliability of data on zooplankton abundance in reef waters might be verified by the comparison of its production with the food demand of zooplankton grazers in its environment. Alldrege & King (1977) found that zooplankton standing stock assessed at that time was less than 100 mg m^{-3} (wet weight) and that this did not match the calculated daily food demands of reef planktivore fauna estimated at 300 to 500 mg m^{-3}. However, this discrepancy should really be 3–4 times greater since only
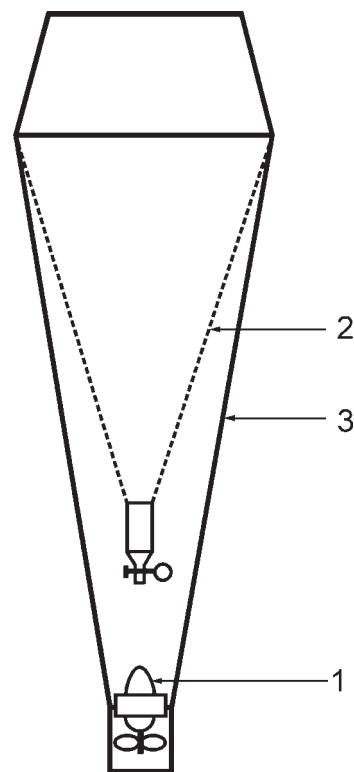

Fig. 7. Appropriate arrangement of plankton net supplied with the current meter; designations: 1, current meter, 2, gauze cone; 3, water impermeable tapestry cone.

zooplankton production, not just the standing stock, is available for grazing. Production of reef zooplankton should be calculated as the sum of production by holoplanktonic copepods plus the production by the whole demersal plankton fraction using corresponding coefficients of their specific production (Table 8) and data on their biomass (Tables 2, 4 & 5). Food demand by the zooplankton-feeding reef fauna could be calculated using the published data on mean biomass of its basic components in reef environments (McWilliam et al., 1981; Sorokin, 1990, 1993) and known values of their daily food rations (Table 8). For example, in a deep lagoon measuring 15 m deep with a sandy bottom the zooplankton wet biomass might be evaluated at 30 g m^2 meaning that the holoplanktonic copepods contribute $\sim$10 g m^{-2} and the benthoplanktonic demersals 20 g m^{-2}. Correspondingly, its production should approach 3 g m^{-3} d^{-1}. The food demand of zooplankton feeding animals in the lagoon should approach 3.5 g m^{-2} (wet weight) being contributed to by the Planktivore fish and crustacean demersals (biomass 30 g m^{-3}, food ration $\sim$2 g m^{-2} d^{-1}), and by benthic zooplankton grazers like resident fish, crustaceans, bryozoans and zoantharians (meat biomass $\sim$20 g m^{-2}, food demand between 1 and 1.5 g m^{-1}). However, zooplankton production by its maximal biomass of 10 to 20 mg C m^{-3} was claimed in the above mentioned publications as being expected at 2 to 4 mg C m^{-3}d or around 0.3–0.6 g m^{-2} d^{-1}of wet weight. This level of zooplankton production is 5–10 times less than the calculated food demand of zooplankton feeding fauna, thus suggesting a gross undercatch with the improved net tow technique, to say nothing of the most commonly used standard net tows.

The most abundant planktivore fauna is found in shallow habitats within a depth-range of 2 to 5 m with bottoms covered with corals, coral rubble and macrophytes. Its principal components are small planktivore fish, fish larvae, corals, hydroid, zantharians, bryozoans and ascidians. Their mean biomass might be assumed at around 15 to 20 g m^{-2} (McWilliam et al., 1981; Sorokin, 1993). Their food demand should approach 1.5–2 g m^{-2}d^{-1} of wet weight. Basic food sources to cover this demand might be created by the whole demersal community hidden in the bottom substrates during the daytime. This production should approach 1–2 g m^{-2}d^{-1} of wet biomass by the biomass of demersals 20 to 40 g m^{-2} (see Tables 4 & 5). This source of food is accessible for the planktivore fauna, when a significant part of the demersal community ($\sim$20 to 40%) migrates at night into the water column (Glynn, 1973; Hobson & Chess, 1978; Harmelin-Vivien, 1981; Robertson et al., 1988). Indeed, bentho-planktonic demersals dominate in the gut content of reef fish (Harmelin-Vivien et al., 1988). Balance calculations based on the adequately assessed zooplankton standing stock including the whole community of demersals show that their joint production is sufficient to meet the food demands of abundant and diverse planktivore fauna on the coral reefs (Table 9). The realistic evaluation of plankton abundance in reef waters has another important aspect which remains ignored. The nutrition efficiency in planktivore animals critically depends upon the food concentration (Panov & Sorokin, 1967; Gaudi, 1974; Petipa, 1981; Sorokin, 1993, 1999). An optimal food concentration ranges between 0.5 and 1.0 g m^{-3} of wet biomass. This level is roughly the same in filter feeders and predators. With a concentration 0.2 to 0.3 g m^{-3}, the assimilated food covers only the respiration losses (the 'threshold' concentration). Below this threshold,

there is inadequate nutrition for survival. A zooplankton concentration in the GBR waters of less than 250 mg m^3 of wet biomass reported in several publications (Hamner et al., 1988; Roman et al., 1990; McKinnon, 2005) is less than the threshold, which suggests it was grossly underestimated. In reality, even the daytime zooplankton concentration in the deep lagoon and in the estuarine areas approaches the optimal 0.3 to 0.5 g m^{-3}.

Hamner et al. (1988) suggest that planktivore fish live mainly over the reefs and thus can collect zooplankton from a large volume of water and while passing over it they could acquire enough food despite the low concentration of zooplankton in this water (Roman et al., 1990). This is not correct. First, the planktivore fish and especially the fish larvae, are not only concentrated over the reef ridges, but are randomly spread in the deep lagoon, where the biomass of fish is around 160 g m^{-2}, while over the reef ridges it is close to 200 g m^{-2} (Williams & Hatcher, 1983). Secondly, the fish catch zooplankton, which are always in motion. This makes no difference whether the water or the fish is moving. Only the food concentration can really influence the rate of nutrition (Petipa, 1981).

The standing stock of zooplankton contained in waters of the GBR lagoon, when appropriately quantified, is measured from 15 to 30 g m^{-2} of wet weight (accounting for demersals). Annual production would be expected roughly at 6000 kg ha^{-1}. This production can support the annual production of only planktivore fish at 500–700 kg ha^{-1}. Moreover, GBR reefs and lagoon are the feeding grounds for fry of many oceanic and coastal benthic and pelagic fish (Davis & Birdsong, 1973; Russ, 1984; Dredge, 1988; Hamner et al., 1988). From this viewpoint, an abundant zooplankton stock on the GBR shelf might be recognized as having a greater economic value than, for example, tourism.

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